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Effects of intertidal height and infestation by Fabia Subquadrata Dana on glycogen, lipid and body component indices of Mytilus Californianus Conrad

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EFFECTS OF INTERTIDAL HEIGHT AND INFESTATION BY *FABIA SUBQUADRATA* DANA ON GLYCOGEN, LIPID, AND BODY COMPONENT INDICES OF *MYTILUS CALIFORNIANUS* CONRAD

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by

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Effects of Intertidal Height and Infestation by *Fabia subquadrata* Dana on Glycogen, Lipid, and Body Component Indices of *Mytilus californianus* Conrad

Gregory Anderson

As our knowledge of bivalves has increased, so has information about their parasites. Most studies of bivalve parasites have been devoted to groups infesting commercially important mollusks, notably trematodes and copepods. Another group of bivalve symbionts which has been known since the early nineteenth century is the brachyuran genus *Pinnotheres* Latreille, 1802 (commonly known as pea crabs). The generic name was given because of the belief that the crabs were predators upon the scallops in which they were most frequently found (Pearce, 1966). However, Stebbing (1893) suggested that instead of acting as predators, the crabs were in fact serving as guards for their hosts.

Despite the global distribution of pinnotherids, comparatively little is known of their biology. Although a few cases of severe damage to oyster and mussel crops have been reported,

relatively little information has been gathered concerning the relationship between pinnotherids and their hosts. Infestation of the California sea mussel, Mytilus californianus Conrad by the pea crab Fabia subquadrata Dana was recorded by Wells (1940), yet it was not until recently (Pearce, 1966) that the biology of the crab was described in detail. Fabia subquadrata inhabits the mytilid mantle cavity, maintains its position by gripping a ctenidium with its dactyls, and carries on what likely is a nearly continuous competition with its host for mucus-entrapped plankton and other filterable food. Despite the dominance of M. californianus in the temporate eastern Pacific intertidal zone (Paine, 1974), there has been only one investigation (Anderson, 1975) of the mussel-crab interaction. While many authors have speculated on the nature and severity of the effects F. subquadrata and other pinnotherids may produce in their hosts, the only well-documented and repeatedly observed result of infestation is irritation and erosion of the hosts' ctenidia, and irritation of some adjacent tissues. The earliest reports of pinnotherid associations (Stebbing, 1893; Wright, 1917; Rathbun, 1918; Wells, 1928, 1940; Freaml, 1943) contain only the most casual observations of host-symbiont interactions, as well as considerable unfounded speculation. In more recent publications (Orton, 1921; Overcash, 1946; Berner, 1954; Cristensen & McDermott, 1958; Pearce, 1962; Seed, 1969a,b,c) judgements as

to the degree of harm the host is thought to suffer as a result of infestation are based primarily upon unaided visual observations of host tissues and/or behavior, while ignoring the possibility of relatively longer-term consequences. Some authors have attempted to understand crab-bivalve associations by assessment of physiological impacts (Kruczynski, 1972; Dix, 1973; Jones, 1977) of the crab on its host.

Establishment of the benefit or harm which a symbiont may confer upon its host requires careful selection of ecologically meaningful criteria upon which such a judgement may be based. The present study attempts to determine, through observation of mussel fecundity and biochemical condition, the extent to which F. subquadrata may affect M. californianus populations. Periodic reproductive activity and gametogenesis are significant energy-demanding events. Periods of reproduction are often accompanied by major changes in body tissue composition as biochemical reserves are oxidized or converted to gametes and supportive tissues (Lawrence et al., 1966; Giese, 1969). Some of these biochemical changes may be followed indirectly using "body component indices" which are organ weights adjusted to account for differences in specimen size. Considerably more information may be gained, however, if the content of metabolic reserve materials (glycogen and lipid) of the affected organs is determined simultaneously. Such combined information

makes possible the localization of biochemical "reserve depots", and estimation of the organism's biochemical preparedness for coping with energetically demanding events. When applied to stressed organisms, whether the stressor be environmental (e.g. low food availability, temperature extremes) or biological (e.g. infestation by a parasite), the impact of that stress on the organism's well being, at least in relative terms, may be assessed.

Mytilus californianus is distributed vertically through a wide intertidal range (Chan, 1973), and therefore exposed to a continuum of height-related environmental stressors. It was anticipated that if reproductive and/or biochemical responses to such physical stressors were to be observed, their direction and magnitude would be not only of ecological significance, but also of assistance in the interpretation of the impact F. subquadrata has upon the physiology of its host.

Materials and Methods

Large samples (ca. 300 - 400 individuals) of mussels Mytilus californianus were collected at approximately monthly intervals for thirteen months beginning in July, 1973. Collections were made each month at two vertically-separated sites ("High" and "Low") which differed in intertidal elevation by 1.5 meters

and were located on a rocky outcropping (38° 18' N) adjacent to Bodega Head, Bodega Bay, California.

Mussels were removed from the substratum, covered with moistened toweling, and taken to the laboratory. The time between collection and arrival at the laboratory was always less than two hours. The mussels were then rough-sorted by size, rasped free of epibiotic organisms, and frozen at -20°C in sealed, triple-layer polyethylene bags.

For analysis, mussels were thawed in small groups at room terperature and dissected immediately. Approximately equal numbers of males and females were used within each of three classes, viz: low zone, high zone, and high zone mussels infested with Fabia subquadrata. Sex usually could be determined by visual assessment of carotenoid content (see Campbell, 1969; Bartlett, 1972; and Griffiths, 1977) but gonad smears were also examined at 400X. Specimens were dissected into the following organs or body components: foot, gills, gonad-mantle (referred to as "gonad"), thickened ventral portions of the mantle (referred to as "mantle"), anterior and posterior adductor muscles, digestive gland, and remainder (referred to as "viscera").

Immediately following removal from the body, components were placed in tared polyethylene containers (the larger and thicker pieces being first sliced repeatedly with a scalpel to facilitate rapid release of moisture) and dried to constant weight at 85°C (Lovegrove, 1966) under air in a mechanical

convection oven. The oven was always preheated to drying temperature to hasten tissue temperature rise in order that enzymatic and microbial degradation of tissues might be halted quickly. Twenty-four hours was found to be a drying period adequate to achieve constant weight.

Dried components were cooled to room temperature in desiccators over indicating Drierite, which was regenerated prior to each use, and weighed on an analytical balance to the nearest tenth milligram. Calculations were made of the net weight of each organ, those weights summed (sum="body dry weight") and each divided by the body dry weight. These data are expressed as arcsin proportions and referred to as "body component indices" (Giese, 1969). Thus the gonad index is that portion of the dry body weight attributable to gonadal material. This data allows relative weight comparisons of organs between mussels of different sizes.

All biochemical determinations were made on tissues which had been ground in a glass-glass Ten Broek tissue grinder. Drying, following the cell disruption inherent in the freezing process, rendered most tissues sufficiently friable to allow grinding directly in the tissue grinder. Large or otherwise difficult tissues, such as "viscera", were generally first ground with a porcelain mortar and pestle and then the Ten Broek grinder.

Seven milliliters of 2:1 (V/V) chloroform:methanol were added to the tissue grinder after the weighed tissue sample. If the tissue had first been ground in a mortar, the solvent, in two portions, was used to rinse it and the pestle into the tissue grinder. Grinding was continued until no particles greater than grinder clearance (ca. 0.13 mm) remained. Contents were poured into 15 ml conical centrifuge tubes, the grinder rinsed with chloroform/methanol and the volume adjusted to 10.0 ml. Following centrifugation to a compact pellet at approximately 1000 RCF, the solvent was carefully decanted into a small test tube and mixed by vortex with 2 mls of 0.2% sodium chloride in water. The organic phase was then transferred to a small, tared glass vial, the solvent evaporated under partial vacuum, and the net residue taken as lipid. The pellet obtained through centrifugation was subsequently resuspended in 10 mls of 5N NaOH and digested at 100^{o}C for 20 minutes. Aliquots of the hydrozylate were taken for dilution and determination of glycogen.

Glycogens (Stetten & Stetten, 1960) were determined on diluted fractions of the alkaline hydrozylate by reaction with 10 mls of 0.2% anthrone in sulfuric acid (Seifter et al., 1950). Optical densities were derived from transmittance readings made at 620 nm on a Bausch & Lomb Spectronic 20. Reagent glucose was used as the standard and a standard curve calculated

by linear regression. Weights thus were obtained as glucose equivalents. Lipid content was calculated similarly, except that no curve reading was necessary.

Prior to statistical analysis, proportional data were subjected to arcsine transformation. The principal statistical treatment was three-way analysis of variance. Because sample sizes within cells were unavoidably unequal, means were used as variates, and second-order interaction terms were assumed insignificant and used in lieu of error terms (Sokal & Rolf, 1969).

Results

Examination of fluctuations in gonad index plots (Fig. 1) reveals that a distinct, apparently cyclical, series of changes occurred during the thirteen-month period of observation. A period of gonadal depletion or quiescence during July, August, and September was followed in fall and winter by gametogenesis as gonadal mass increased to a maximum in February. Beginning the following April and continuing through May, June and July, a precipitous drop of the gonad index was observed, indicating massive spawning; gonad index levels in July of 1974 were similar to those observed the previous July.

It is clear that low and high mussels are synchronous with respect to time and direction of gonad index change (Low-High: $r=0.86$, $n=12$, $p \leq 0.01$), but that the magnitude of change

(or difference in gametic mass generated between quiescent and "ripe" stages) differs significantly, being greater in low zone mussels than in high zone mussels. Correlation coefficients (r) were calculated between high and low mussels' gonad indices using data pairs within months. A significant increase in gonad mass in infested specimens was not observed. During most months, gonads of lower zone mussels were larger than those of high zone mussels. Gonads of infested mussels were smaller than gonads of uninfested mussels. These relationships are most readily observable during those months in which gametogenesis took place, and those in which mussels maintained a ripe condition. The magnitude of differences between classes is minimal and insignificant during the aforementioned summer period of quiescence.

Analysis of variance shows that season, tidal height, and infestation were all significant contributors to the variation of the gonad index (Tables 1 and 2). Sex was not found to significantly effect gonad indices in any class. In low zone mussels, the digestive gland varied inversely over season with the gonad ($r=0.87$, $p\leq0.01$), although in high and infested mussels, significant correlations between these organs were not obtained. Mantle indices in all groups of mussels varied significantly with season ($F_{1,11}=23.52$, $p\leq0.01$) but no trends in variation were observed, and there was no

correlation with gametogenic cycle. Season contributed significantly to the variation of all other organ indices, but no pattern of association with the gonad cycle was detected.

Season, tidal height, sex, and infestation all contributed significantly (Table 3) to variation observed in the levels of tissue lipid and glycogen. Season was a significant factor in the variation of these reserve materials in all organs except the viscera.

Mean gonadal lipid content varied with season, reaching in each of the three classes, maxima and minima which corresponded terporally with maxima and minima of the gonad index (see figures 2 - 4). Males accumulated considerably less lipid in the gonad than did females ($F_{1,11}=21.01$, $p\leq 0.01$), the difference being approximately thirty percent at full ripeness in February and March; in the summer months, when gonads were depleted, a significant difference between sexes was not observed.

Mantle lipid in low zone specimens increased from July through October. In November, as gonadal lipid deposition increased markedly, mantle lipid content declined sharply. This reciprocal relationship was maintained during the period of study as may be seen on inspection of Figure 2. In high and high-infested specimens, significant lipid accumulation in the mantle was not detected prior to the initiation of

intense gametogenic activity. Low zone mussels contained significantly greater amounts of mantle lipid over the entire period of study than did high zone mussels ($F_{1,11}=33.70$, $p\leq0.01$). Moreover, comparison of overall mean mantle lipid contents of high and high-infested specimens by one-tailed "t-test" demonstrates that infested mussels maintain significantly ($t_{11}=2.04$) less mantle lipid throughout the year.

Digestive gland lipid content also varied significantly with season, but variation was not correlated significantly with gonadal fluctuations. Consistent, significant differences were found between classes, however. Thus low zone mussels maintained greater amounts of digestive gland lipid than high zone individuals ($F_{1,11}=27.09$, $p\leq0.01$), which in turn maintained higher levels than infested individuals ($F_{1,11}=7.46$, $p\leq0.025$). Other than in the mantle, the digestive gland was the only organ in which infestation was seen to produce a significant change in lipid level.

A small but significant difference was observed in gill lipid content between low and high zone mussels; the former maintained a slightly higher level throughout the year. Infestation had no discernable effect on gill lipid.

Variations in the glycogen content of the various organs are summarized (see Figs. 5-7, and Table 3). It may be seen that viscera glycogen content was relatively constant throughout the year, and was not effected by tidal height or the

presence of F. subquadrata. Of the remaining organs, as illustrated by the data arrayed in Table 4, the mantle, digestive gland, and quiescent gonadal tissues, taken together, constitute a repository for the bulk of the available or mobile glycogen - that is, glycogen which was seen to vary with season, tidal height, and/or infestation.

Glycogen levels in both the digestive gland and mantle were lower in infested mussels than in uninfested high zone mussels (Digestive gland, $F_{1,11}=72.08$, p 0.001; Mantle, $F_{1,11}=69.31$, $p\leq 0.001$). Moreover, high zone mussels were unable to accumulate as much glycogen in gonadal tissue ($F_{1,11}=5.41$, $p\leq 0.05$), mantle ($F_{1,11}=10.33$, p 0.01), and digestive gland ($F_{1,11}=17.29$, $p\leq 0.005$) as were low zone specimens. Glycogen was deposited during the fall in gonadal, digestive gland, and mantle tissue in relatively large amounts in low zone mussels, and in lesser amounts in high, uninfested specimens. During November and December, as gonadal development intensified and concomitant gonadal lipid deposition occurred, glycogen stores were catabolized and levels returned to their respective yearly minima. In contrast, although infested mussels showed significant glycogen variation with season, they did not accumulate glycogen reserves in significant amounts prior to the onset of the massive lipogenesis necessary for gonadal ripening. In addition, inspection of Table 5 and Figure 1

shows that infested mussels converted considerably less lipid into gametes than did uninfested mussels. Similarly, uninfested high zone mussels deposited less lipid in the gonad than did low zone mussels.

Discussion

The gonad index, a weight- or size-normalized function of gonad mass, has been used often, though with some technical variation, in ecological and physiological studies of mollusks (see for example, Lawrence et al., 1965; Giese, 1962 (Katharina); Gonor, 1972 (Stongylocentrotus); Branch, 1974 (Patella); Hughes, 1970 (Scorbicularia); and Griffiths, 1977 (Choromytilus)). During the duration of the present study (1973-1974), only one distinct peak of the M. californianus gonad index was observed, while in an earlier study of an adjacent population (Dillon Beach, California, $38^{o}15'$ N) Bartlett (1972) concluded M. californianus spawned more or less continuously (1971-1972). Examination of his data, however, shows that the largest proportions of ripe and "partially-recovered" individuals were obtained mostly in the same months of the year during which the gonad index reached its maximum in the present study (i.e. January through March). The apparent discrepancy involves only what is here referred to as the "quiescent" stage

of the gonad cycle. As noted above, gametes were observable in most of the specimens collected each month. Present data are not sufficient to determine whether or not a continuous, low-level discharge of gametes may have taken place. In any case, consideration of the reproductive patterns of Mytilus spp. leads one to the conclusion that both the number of periods of intense spawning activity and the magnitude of pre-spawn gonadal build-up are variable within species and very dependent upon nutritional and environmental factors (Giese, 1959; Bayne, 1976). For example, on the basis of observations of planktonic larvae, Coe (1932) concluded M. californianus spawns mainly in the period June through September. Data extracted from Whedon and Sommer (1938) show that relatively light spawning occurred in early November, and a much heavier and complete spawning during mid-December. Fox and Coe (1943) conclude that spawning is distinctly seasonal, but that the season may vary among years. Young (1946) found that while low-level spawning appeared to occur throughout the year, relatively heavy activity was concentrated in the period between October and March. Many of these authors cited temperature as a primary "triggering" factor in the control of spawning, but other conditions such as plankton blooms and changing light-dark regimes also were thought to do this. It is clear that data from short-term

studies on single or several adjacent populations cannot be used to make generalizations about the timing and other characteristics of reproduction in M. californianus.

In evaluating the biochemical effects of intertidal height and infestation by Fabia subquadrata, it may be presumed that low zone mussels not infested by symbionts are the least-stressed of the mussels investigated; indeed, that they are subject to less physically-induced stress is well known (see Paine, 1974), and there is no reason to suspect pinnotherids of conferring advantage on their hosts. As shown above, low zone mussels deposited greater quantities of glycogen than high mussels, and the latter deposited more than infested specimens prior to the time of most intense gametogenesis. While most classes of marine invertebrates accumulate dispersed lipid as their primary reserve material, bivalves are peculiar in that many are known to store and rely upon glycogens as their principal reserve (Giese, 1969). For example, Donax vittatus catabolizes lipid to meet reproductive demands, but at least some tellinids (Ansell & Trevallion, 1967) store much glycogen but little lipid. Galtsoff (1964) points out that the commercially desirable "ripe" or "fat" oyster (several species are discussed) is not at all fat, but instead contains tissues replete with glycogen which will soon be used to support gametogenesis.

The reproductive consequence of the accumulation of subnormal glycogen reserves prior to the onset of gametogenesis may be interpreted as follows: The absence of detectable differences in biochemical composition of gonad within sexes and among classes strongly suggests that the ratio of gamete numbers to unit of gonad dry-weight was constant among the classes. Since the gametes contain large amounts of lipid, relatively small changes in their numerical abundance in gonadal tissue would likely have been detected. Thus, it may be concluded that high and high-infested mussels which had lower gonadal mass prior to spawning held, and probably shed fewer gametes than the low zone mussels. Similar reasoning may be applied to a comparison of high and high-infested specimens, in which the mussels infested by F. subquadrata produced less gonad. As mentioned earlier, the rise in the gonad index prior to spawning is barely significant in high intertidal mussels infested by F. subquadrata, with which they must compete for nutrition (see Figure 3).

The foregoing results show that while some components of the mussel body are capable of considerable glycogen storage and serve as a ready source of glucose for gametogenesis, other body components such as the viscera (which consists principally of pedal retractor and other musculature), the adductors, and the ctenidia contain low and relatively stable

amounts of glycogen which seem unavailable to the reproductive effort. As may be seen on examination of Table 4, the bulk of the whole-body glycogen in low zone mussels prior to the initiation of intense gametogenic activity was present in those organs (mantle, digestive gland, and quiescent gonad) found to contain "mobile glycogen" stores - that is, glycogen deposits which varied significantly with season and reproductive state.

The metabolic strategy of having glycogen reserves in some parts of the body seems reasonable on consideration that to ensure survival of daily exposure-immersion cycles with concomitant hazards and stresses, M. californianus must conserve sufficient energy to maintain some essential metabolic functions. These include operation of the anterior and posterior adductors (to oppose the force continuously exerted by the hinge ligament), pedal retractor musculature and ctenidial apparatus, each of which likely requires considerable energy, and appears to be essential to daily survival. Thus, despite the possibility of attenuated reproductive output, M. californianus appears to reserve some of its glycogen stores to fuel critical metabolic functions. De Zwaan and Zandee (1972) also found that the glycogen in M. edulis gills and muscle varied little over season in comparison with fluctuations found in other organs.

Seasonal fluctuations in glycogen in many molluscs have

been demonstrated, usually in conjunction with their reproductive cycles (Galtsoff, 1964; De Zwaan & Zandee, 1972b; Comely, 1974; Ansell, 1975), and in response to a variety of natural and artificial stresses (for example, infestation by Mytilicola [Copepoda], Hepper, 1955 and Williams, 1969; nutritive stress, Bayne, 1973 and Thompson, Ratcliffe and Bayne, 1974; temperature stress, Bayne and Thompson, 1970; intertidal exposure [i.e. forced anaerobiosis] De Zwaan and Zandee, 1972). Though many measured only "whole body glycogen" rather than the glycogen content of separate organs, all found glycogen was consumed quickly in response to stress or commencement of gametogenic activity. That glycogen stores are relied upon to such a great extent for provision of the energy necessary to cope with stressful situations lends support to the hypothesis that any factor which causes a reduction of mobile glycogen reserves must increase the probability of mortality.

While lipid content varied considerably with season, only the digestive gland and mantle tissues were found to respond significantly to tidal height and the presence of F. subquadrata. It should be noted that the relationships of lipid contents of the two organs among the three classes was fairly consistent over the year and indicative of a chronic lack of substantial neutral lipid stores in high and infested mussels. Moreover, it was shown that considerably less lipid

is present in mussels which previously had accumulated less glycogen. The interconversion of glycogen to lipid has not been conclusively demonstrated in bivalves, though the occurrence of such conversions is hardly in doubt (Gabbott, 1975). Glycogen is presumed to undergo hydrolysis to a phosphoglucose monomer which is easily converted glycolytically to acetyl-Co-A; during neolipogenesis, the latter compound is converted to a fatty acyl-Co-A and esterified with glycerol in the production of mono-, di- and triglycerides, by far the most predominant of the storage lipid classes. Thus, the lipogenic activity essential to mytilid gonadal buildup is largely financed by catabolism of stored glycogen.

Table 1

Analysis of variance of gonad index with intertidal height, month, and sex as treatments

Source	df	MS	Fs
Height	1	224.94	180.74 *
Month	11	76.28	61.29 *
Sex	1	2.65	ns
Height X Month	11	4.12	3.31 *
Height X Sex	1	0.26	ns
Month X Sex	11	1.68	ns
Height X Month X Sex	11	1.24	

* Signifies $p \leq 0.05$

Table 2

Analysis of variance of gonad index with infestation by F. subquadrata, month, and sex as treatments

Source	df	MS	Fs
Infestation	1	224.94	180.74 *
Month	11	76.28	61.29
Sex	1	2.65	ns
Infestation X Month	11	4.12	3.31
Infestation X Sex	1	0.26	ns
Month X Sex	11	1.68	ns
Infestation X Month X Sex	11	1.24	

*Signifies $p \leq 0.05$

Table 3

Summary of analyses of variance in glycogen and lipid content of *M. californianus* tissues. Treatments are intertidal height, season, infestation, and sex. A plus (+) indicates significance ($p \leq 0.05$), and a minus that significant effects were not observed ($p \leq 0.05$).

Glycogen Content

	Height	Season	Infestation	Sex
Gill	+	+	+	-
Gonad	+	+	-	-
Mantle	+	+	+	-
Adductor	-	+	-	-
Digestive Gland	+	+	+	-
Viscera	-	-	-	-

Lipid Content

	Height	Season	Infestation	Sex
Gill	+	+	-	-
Gonad	-	+	-	+
Mantle	+	+	-	-
Adductor	+	+	-	+
Digestive Gland	+	+	+	-
Viscera	-	-	-	-

Table 4

Gonad lipid content during three months immediately preceding spawning. Data are mean (mg) + 1 s.e. (n)

	Females	Males
January		
Low	261.5 + 29.13 (8)	172.0 + 28.28 (7)
High	174.2 + 22.63 (4)	138.9 + 18.86 (6)
High, Infested	133.4 + 39.16 (3)	135.7 + 45.77 (5)
February		
Low	460.6 + 75.57 (6)	296.4 + 18.16 (4)
High	262.2 + 9.68 (6)	300.6 + 42.93 (4)
High, Infested	218.3 + 43.35 (3)	140.7 + 20.26 (5)
March		
Low	332.2 + 41.38 (5)	296.0 + 67.30 (4)
High	184.8 + 22.10 (6)	82.13 + 14.45 (4)
High, Infested	81.35 + 14.70 (3)	83.17 + 10.66 (4)

Figure 1. Gonad index, sexes combined

GONAD INDEX, SEXES COMBINED

Figure 1

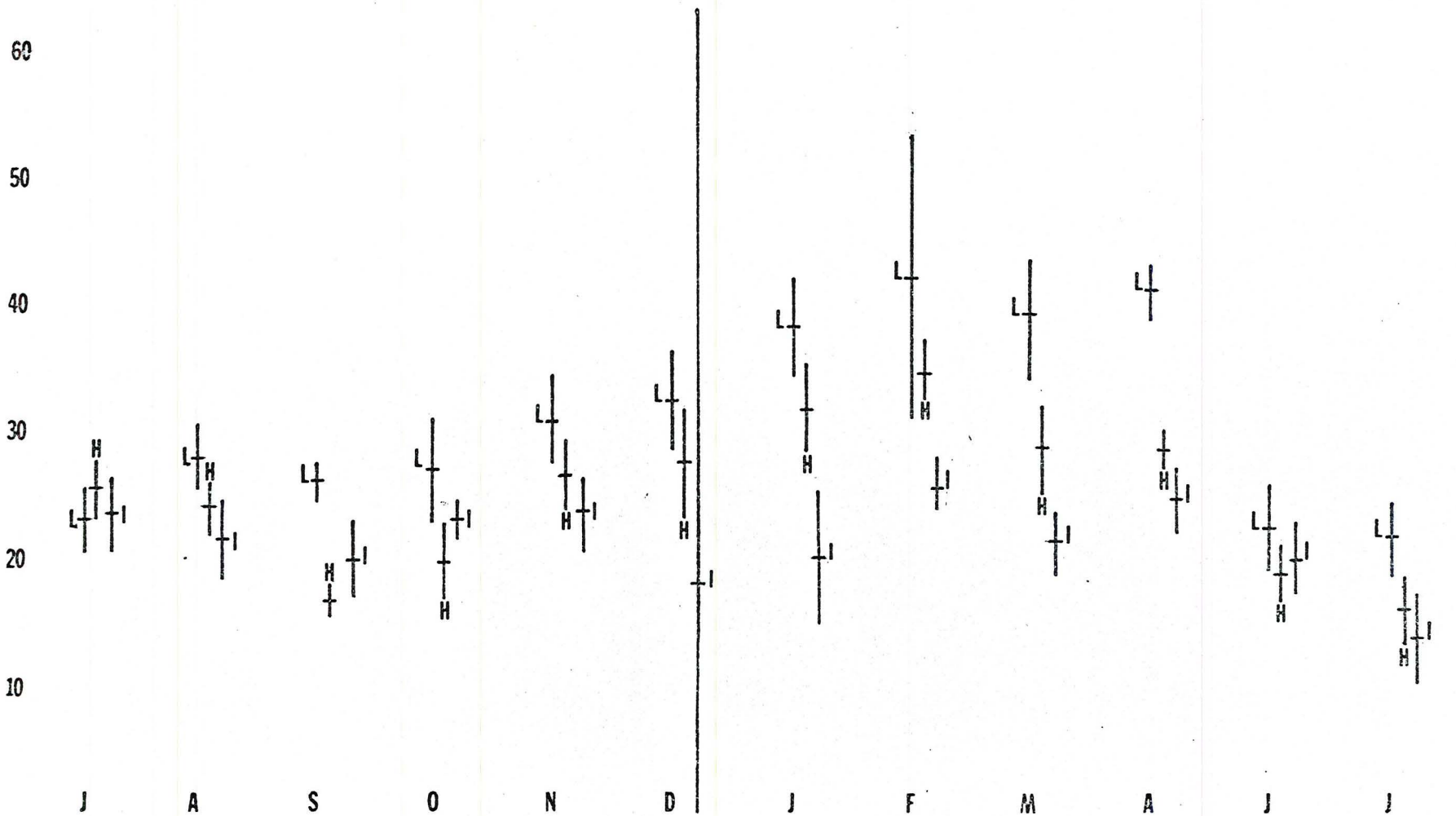
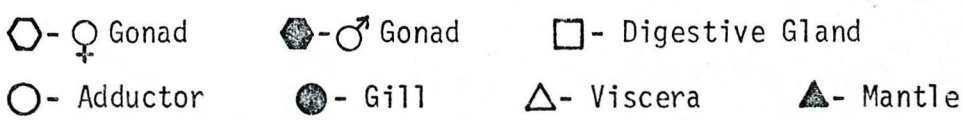


Figure 2. Organ lipid (μg/mg), low zone.



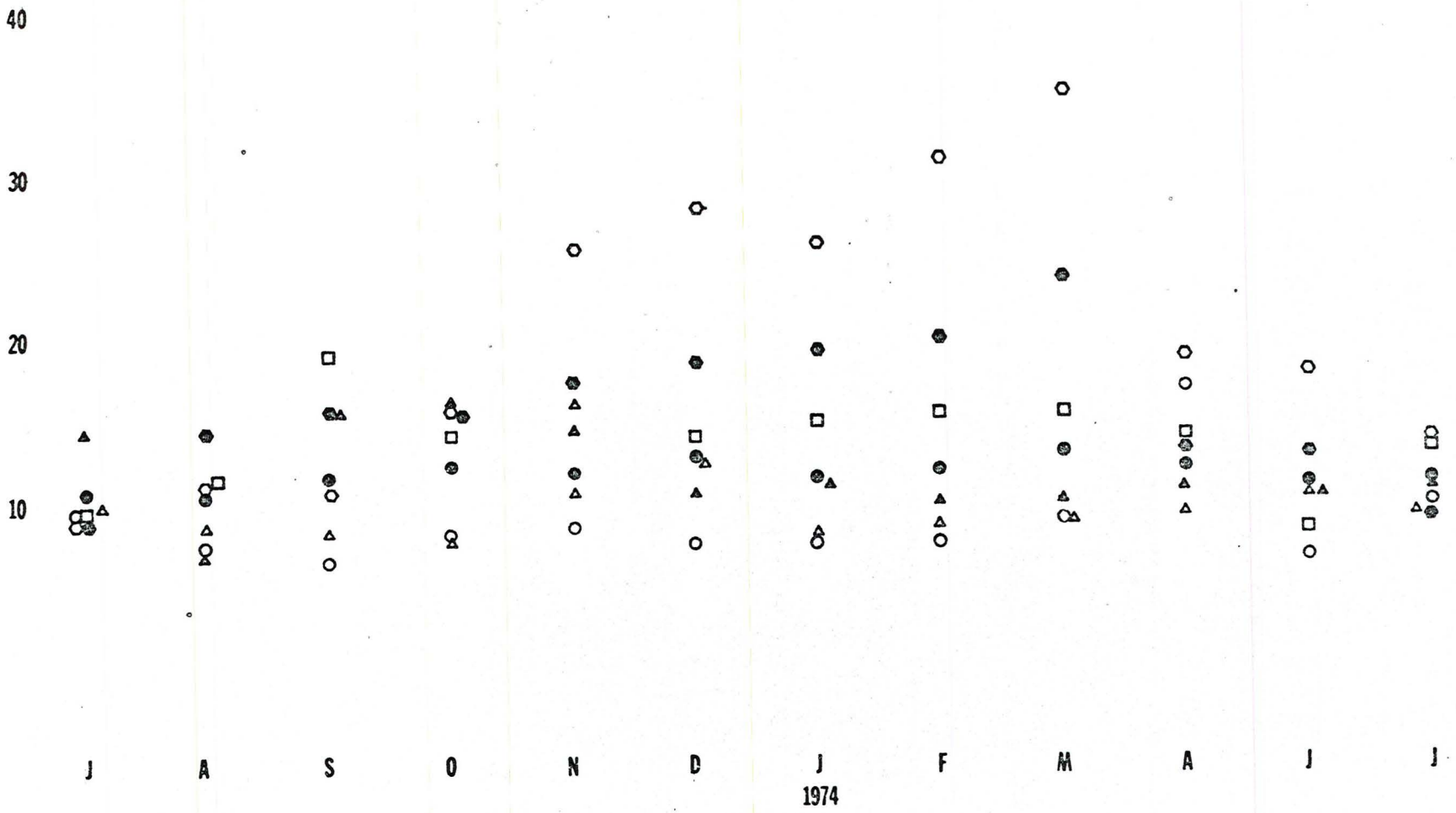


Figure 2

Figure 3. Organ lipid (μg/mg), high infested.

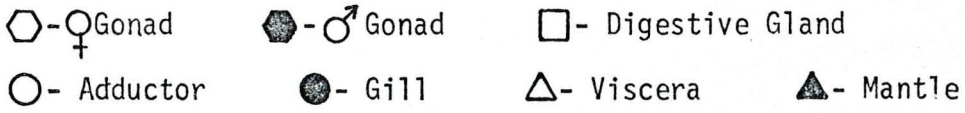
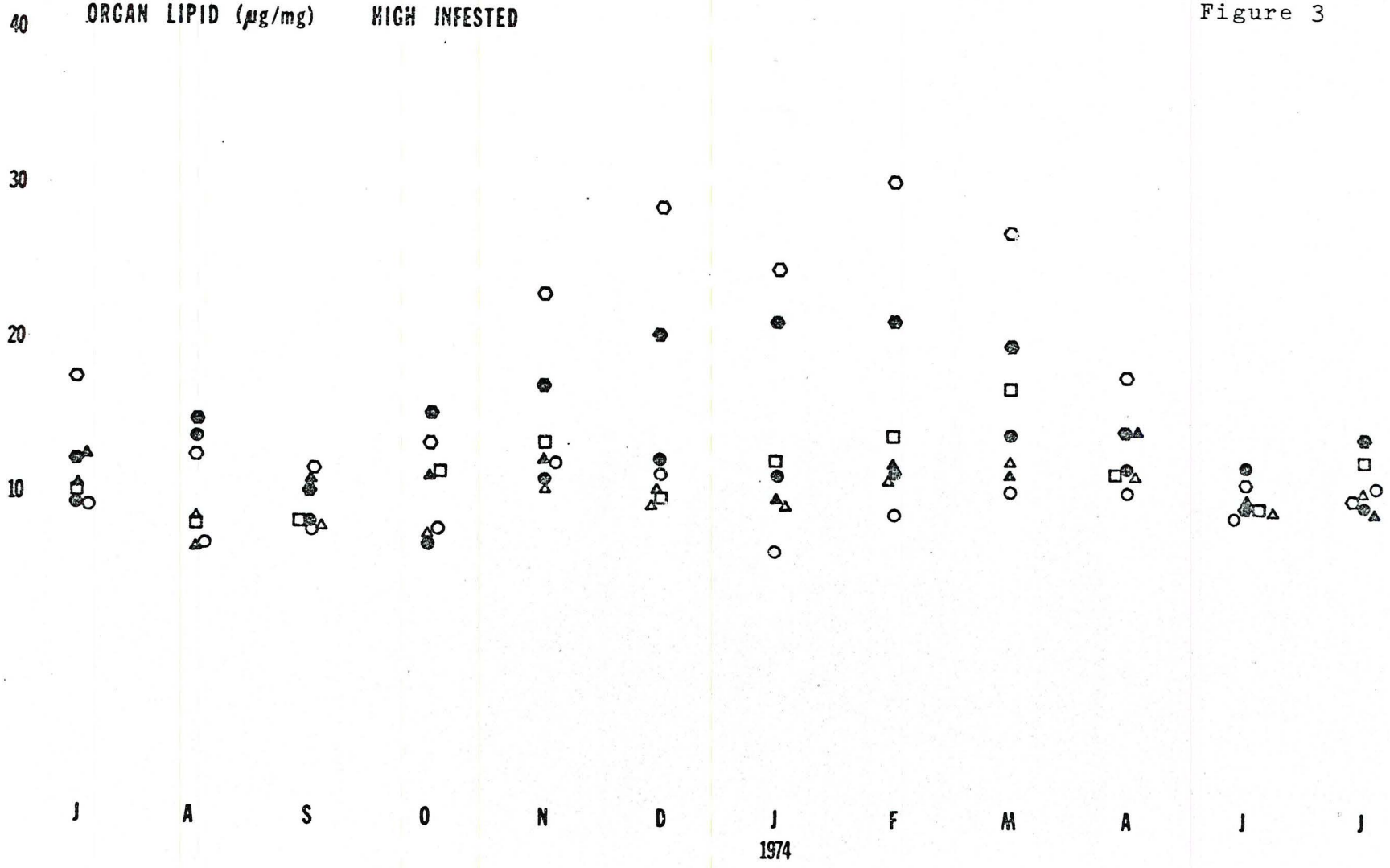


Figure 3


40
ORGAN LIPID (µg/mg)
HIGH INFESTED
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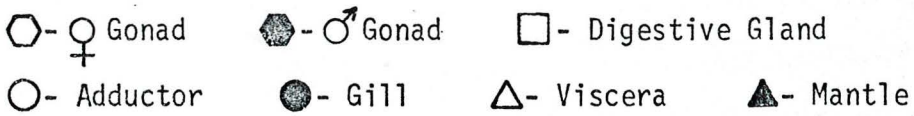
1974

Figure 4. Organ lipid (μg/mg), high zone.



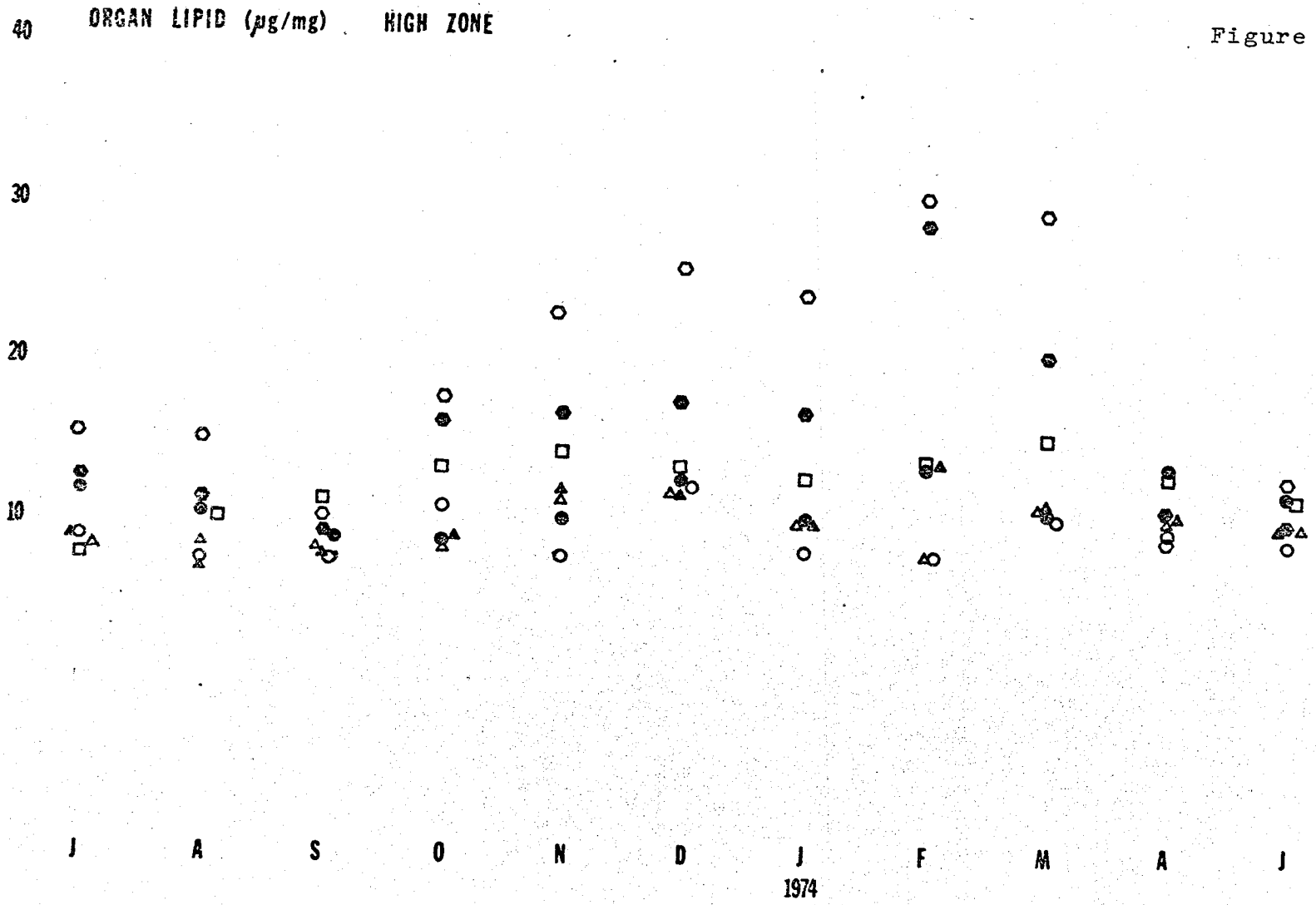
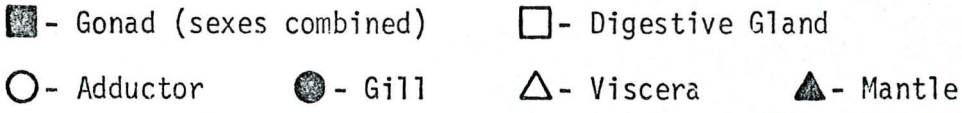
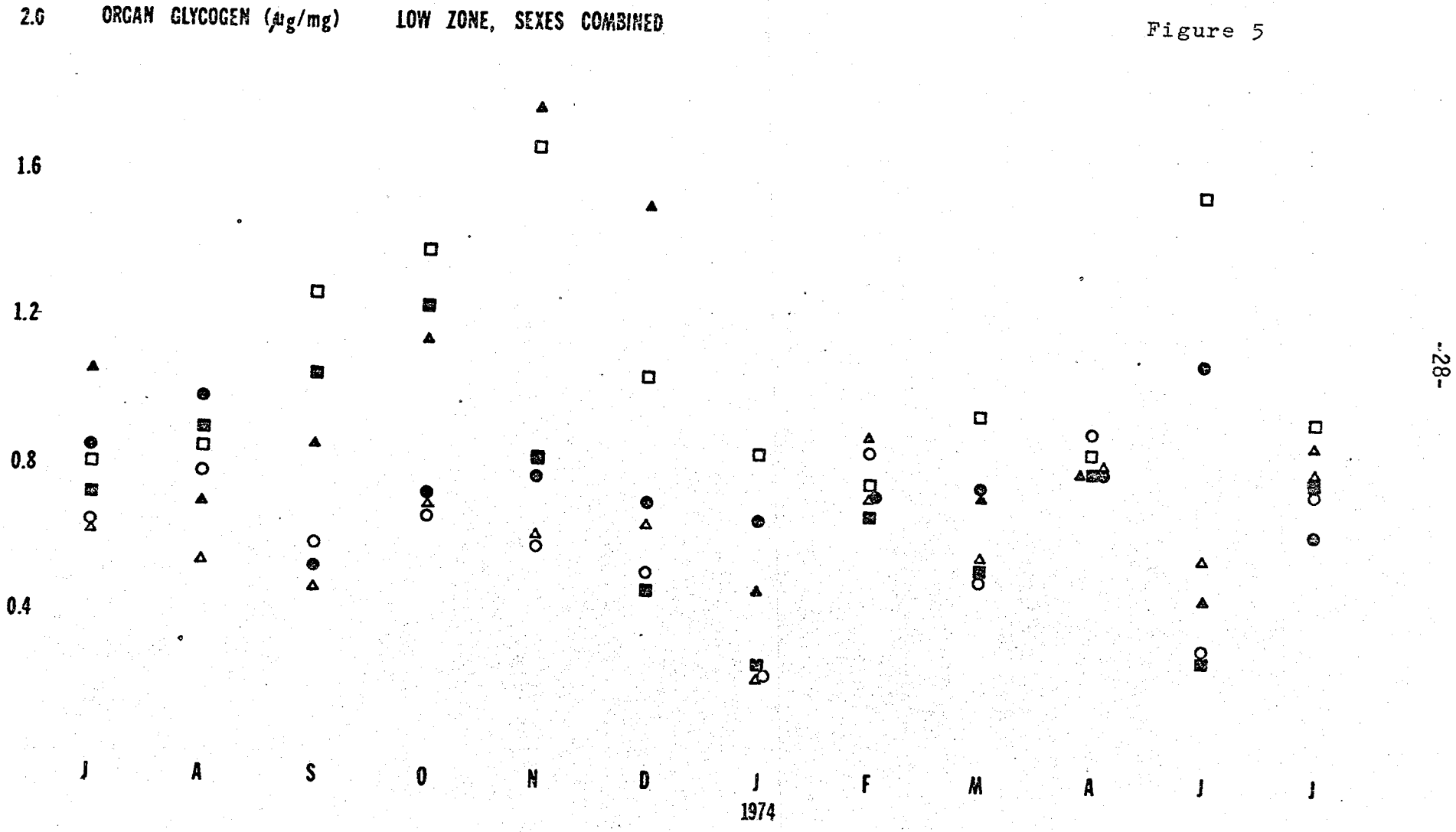


Figure 4

Figure 5. Organ glycogen (μg/mg), low zone, sexes combined.




2.0
ORGAN GLYCOGEN (µg/mg)
LOW ZONE, SEXES COMBINED
1.6
1.2
0.8
0.4
J
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J
F
M
A
M
J
1974

Figure 5

Figure 6. Organ glycogen (μg/mg), high zone, sexes combined.

■ - Gonad (sexes combined) □ - Digestive Gland

○ - Adductor ● - Gill △ - Viscera ▲ - Mantle

Figure 6

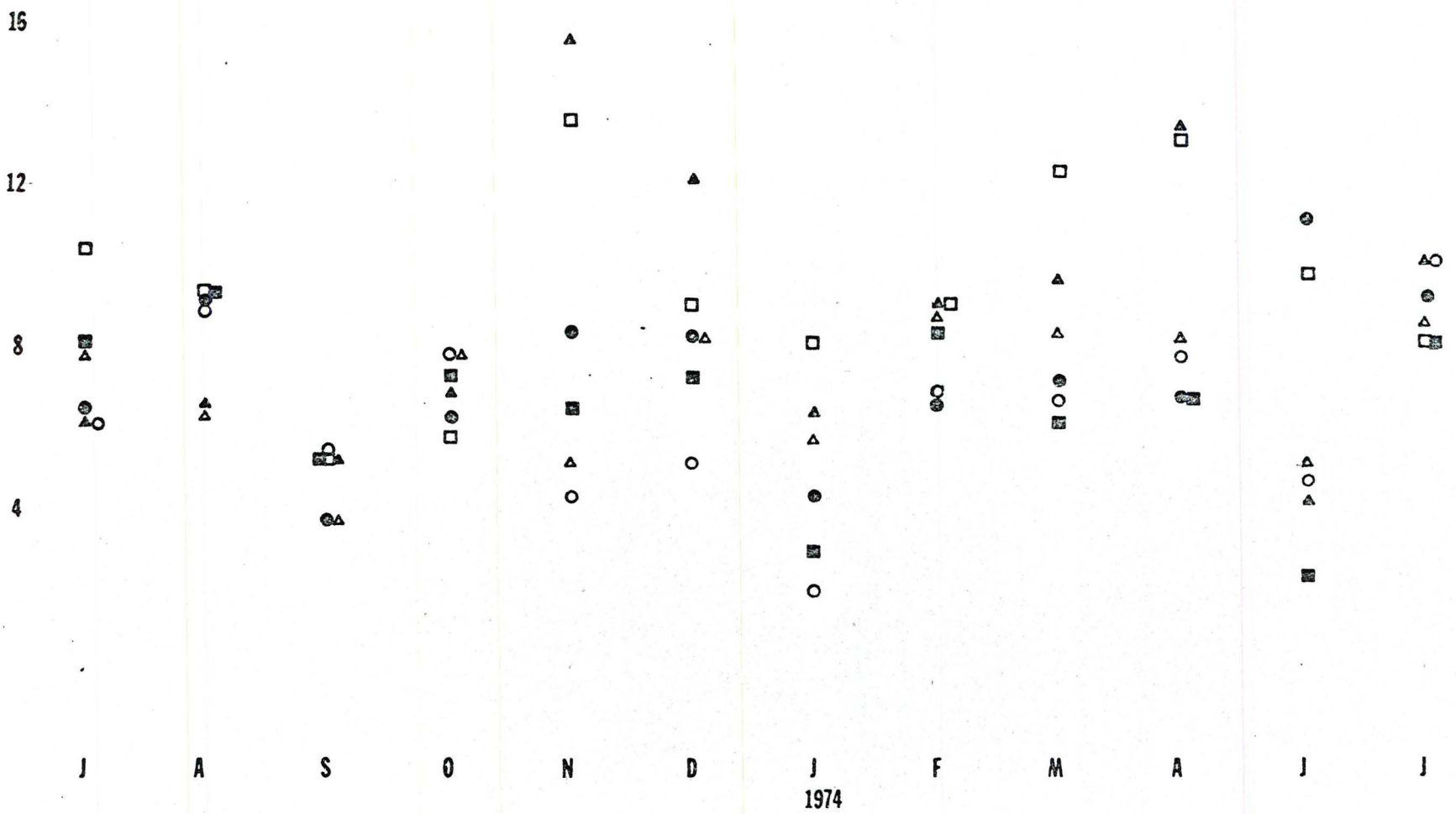
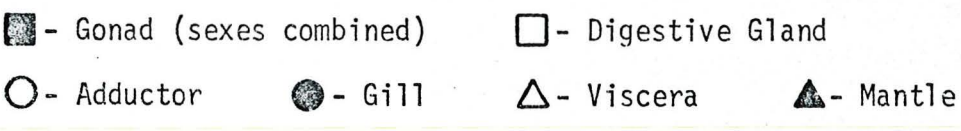
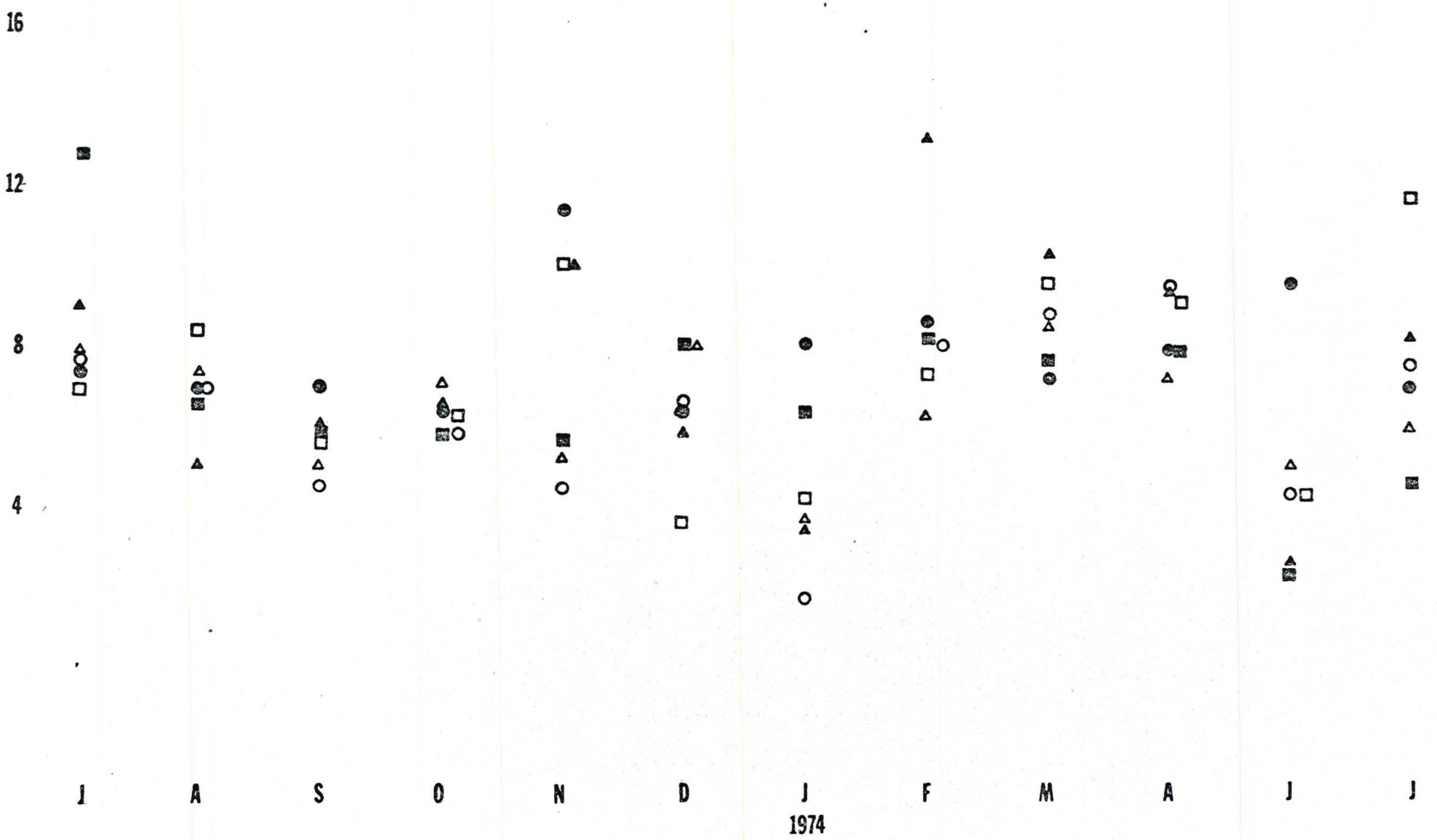

ORGAN GLYCOGEN (µg/mg) HIGH ZONE, SEXES COMBINED
16
12
8
4
J
A
S
O
N
D
J
F
M
A
J
J
1974

Figure 7. Organ glycogen (μg/mg), high infested, sexes combined.



ORGAN GLYCOGEN (µg/mg) HIGH INFESTED, SEXES COMBINED

Figure 7



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